J. HYM. RES.
Vol. 17(1), 2008, pp. 86–109

Patterns of Usage of Snail Shells for Nesting by Wasps (Vespidae: Masarinae and Eumeninae) and Bees (Megachilidae: Megachilinae) in Southern Africa

Sarah K. Gess and Friedrich W. Gess

Department of Entomology, Makana Biodiversity Centre, Albany Museum, Grahamstown, 6139 South Africa; email: s.gess@ru.ac.za and f.gess@ru.ac.za

---

Abstract.—The present contribution to the knowledge of the use of snail shells for nesting by Hymenoptera in southern Africa adds considerably to the earlier contribution by the authors on this subject. It establishes that the strategy of nesting in sand-filled shells is commonly employed by *Quartinia* Ed. André (Vespidae: Masarinae) throughout the sandy winter rainfall areas. It records additional rearings from *Quartinia* nests of *Allocoelia* Mocsáry (Chrysididae), *Tricholabiodes* Radoszkowski and an undescribed genus (Mutillidae), and *Apolysis hesseana* Evenhuis and Greathead (Bombyliidae). Nesting by *Tachysphex hermia* Arnold (Crabronidae: Larrinae) in a sand-filled snail shell is recorded for the first time. It establishes that the distribution of use of snail shells for nesting by bees coincides with and extends along the south coast east of that of *Quartinia*. The bees (Megachilidae: Megachilinae) involved are osmiines, species of *Wainia (Caposmia)* Peters and *Hoplitis (Anthocopa)* Lepeletier and Serville, and anthidiines, including *Afranthidium (Afranthidium) hamaticauda* Pasteels, all cavity nesters using empty snail shells. The only other aculeate recorded as using empty shells is *Alastor ricae* Giordani Soika (Vespidae: Eumeninae). Parasitism in bee nests in snail shells is uncommon. Only *Chrysis* Linnaeus (Chrysididae) and Eupelminae (Chalcidoidea: Eupelmidae) were found, each at only two sites. The preferred snail shells are those of several species of *Trigonephrus* Pilsbry (Dorcasiidae) on the west coast and in the desertic areas and of *Tropidophora ligata* (Müller) (Pomatiidae) along the south coast to the east, all indigenous species. In some areas the habitats of these have been invaded by an exotic snail, *Theba pisana* (Müller) (Helicidae). Shells of this snail are used to a limited extent by the smaller nesters in snail shells. This exotic snail presents a threat to the indigenous snails and to the snail shell nesters. In some areas ongoing coastal development is also a threat.

The bulk of the knowledge of the use of snail shells for nesting by aculeate Hymenoptera prior to Gess and Gess (1999) was confined to the northern Hemisphere where the use of empty snail shells by bees that do not excavate nesting burrows, but search out pre-existing burrows in which to construct their brood-cells, is widely known and is practised in a variety of habitats by: in the Nearctic two species of Osmiini (*Osmia* and *Ashmeadiella*); and in the Palaearctic 14 species of Osmiini (*Osmia* and *Hoplitis*), three in Britain, five in Central Europe, three in the Mediterranean, four in Eurasia and one in Japan, and for one species of Anthidiini, a species of *Rhodanthidium*, from the Mediterranean into Asia Minor (Extracted from O'Toole and Raw 1991 and Bellman 1995). Minimal records for southern Africa prior to 1999 were observations, not supported by specimens, of a "Eumenid-wasp" and an "*Anthidium*-bee" nesting in *Trigonephrus* shells (Hesse 1944) and a record, supported by specimens, of nesting by *Wainia (Caposmia) elizabethae* (as *Osmia* sp. in Gess and Gess 1988 and as *Hoplitis* sp. in Gess and Gess 1997) in shells of *Tropidophora ligata* collected by Ed. Callan on coastal sand-dunes at Saltvlei, Port Alfred, Eastern Cape.

The 1999 study investigated the use by wasps, bees and spiders of empty and sand-filled shells of *Trigonephrus* at 10 sites in seven desertic winter-rainfall areas in southern Africa from immediately north of the Orange River east of Oranjemund south to Wallekraal inland of Hondeklip Bay (Gess and Gess 1999). The principal users of the shells were found to be spiders constructing silk-bag nests and two nesting categories of aculeate Hymenoptera: burrow excavators using sand-filled shells, two species of *Quartinia*; and nesters in pre-existing cavities using empty snail shells into which are brought in nesting materials, a eumenine wasp, *Alastor ricae*, and megachilid bees – single species each of *Wainia* (*Caposmia*) (as *Wainia* (*Wainia*) and *Hoplitis* (*Anthocopa*) (Osmiini), and *Afranthidium* (*Afranthidium*) *hamaticauda* (as *Afranthidium* (*Oranthidium*) and in Gess and Gess 2007 as *Afranthidium* (*Afranthidium*) *ablusum*) (Anthidiini). Recorded associates were undescribed *Tricholabiodes* (Mutillidae: Sphaeropthalminae: Dasylabrini), undescribed *Allocoelia* (Chrysididae: Chrysidinae: Allocoeliini) and *Apolysis* (Bombyliidae: Ursiinae: Ursiini) from *Quartinia* nests, Eupelminae (Chalcidoidea: Eupelmidae) reared from cocoons of *H. (Anthocopa)* and *Trichodes aulicus* Kl. (Coleoptera: Cleridae) from a shell used for nesting by *W. (Caposmia)*.

A sample of 13 *Trigonephrus* shells from the Groot Derm in the "Yellow Dunes, part of the northern Succulent Karoo, Northern Cape", collected by members of the BIOTA-Southern Africa Project, directed from Hamburg, Germany. From these unopened shells deposited in the Natural History Museum, Berlin, *Hoplitis* sp., *Alastor ricae* and a chrysidid wasp, *Chrysis grootdermensis* Koch emerged (Koch 2006).

Since 1999 the authors have extended their sampling of *Trigonephrus* shells northwards in the winter-rainfall desertic areas of southwestern Namibia to the northern limit of the distribution of the snails (23 additional sites) and southwards, principally along the coast to Cape Town (14 additional sites). Where present they have investigated the use of the shells of other land snails–an invasive exotic snail *Theba pisana* along the coast from Port Nolloth southwards to Cape Town and eastwards along the south coast to Riet River Mouth in the Eastern Cape Province (15 sites) and an indigenous snail *Tropidophora ligata*, the shells of which were encountered only on the southeastern coast. Neither large numbers of snail shells nor use of snail shells for nesting was discovered in any other areas during the course of fieldwork conducted throughout the semi-arid to arid areas of southern Africa–of particular interest, nowhere in the sandy areas of the Namib Desert north of Lüderitz, or from the Kuiseb River north to Terrace Bay nor in the southern Kalahari, that is desertic areas outside the winter rainfall area. The results of this more extensive study are presented in the present paper together with the earlier contributions giving an account of the present knowledge of nesting by aculeate wasps and bees in snail shells in southern Africa.

Names of authors of taxa are used in the body of the paper only if they are not available from the abstract and appendix.

METHODS

Sampling sites.—The shells of medium to large terrestrial snails, are abundantly available, empty and sand-filled, in the desertic winter rainfall areas and the areas of sandy coastal dunes of southwestern Africa, where they offer abundant secure microhabitats in these areas of sparse low vegetation and unstable, often windswept sand (Figs. 2–5). Generally Asteraceae, Aizoaceae: Mesembryanthema (formerly Mesembryanthemaceae) and monocotyledonous geophytes were represented and in the northern desertic areas generally in addition Geraniaceae (*Sarcocaulon*), Neuradaceae (*Grielum*) and Zygophyllaceae (*Zygophyllum*). Papilionoideae (Fabaceae) were present at some sites. All snail shell sampling sites, except the more eastern ones on the coast lie within the winter

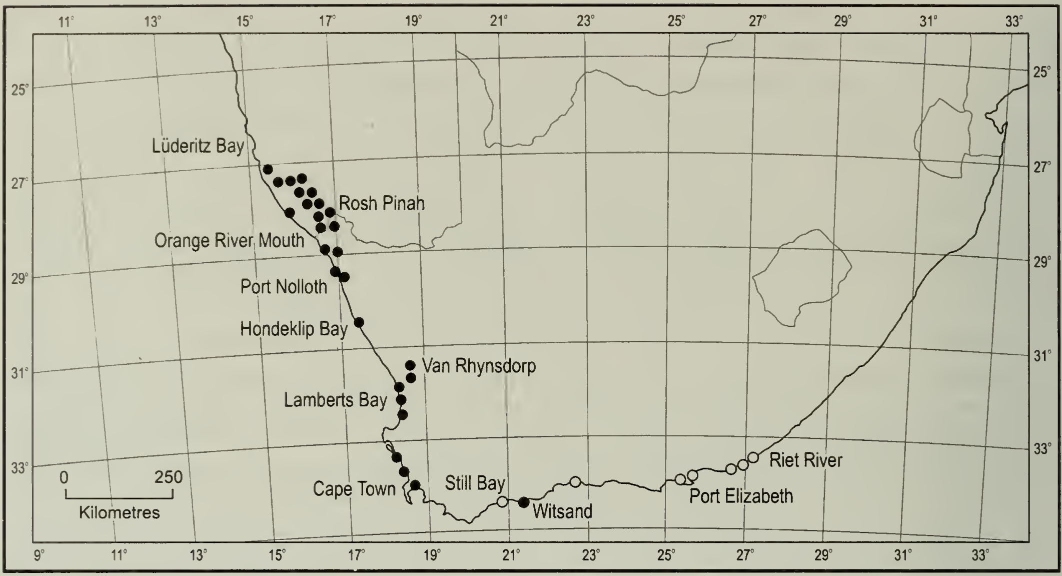


Fig. 1. Distribution of snail shell sampling sites in southern Africa. Solid spots indicate sites at which *Quartinia* (Vespidae: Masarinae) was found nesting in snail shells.

rainfall area. Sampling sites were selected throughout this area (Fig. 1, map, and Appendix, list of all sites with their co-ordinates).

Identity, size and distributions of snail shells sampled.—Snail shells sampled were all of terrestrial snails (Mollusca: Gasteropoda) (Figs. 6–11) – several species of

Fig. 2, The Klingı artberge, a sparsely vegetated desertic area in southwestern Namibia.

Fig. 3. Near Lutzville southwest of Vanrhynsdorp in the Western Cape, sandveld.

Fig. 4. Donkinsbaai, southwest coast, Western Cape, well vegetated dune slack behind foredunes.

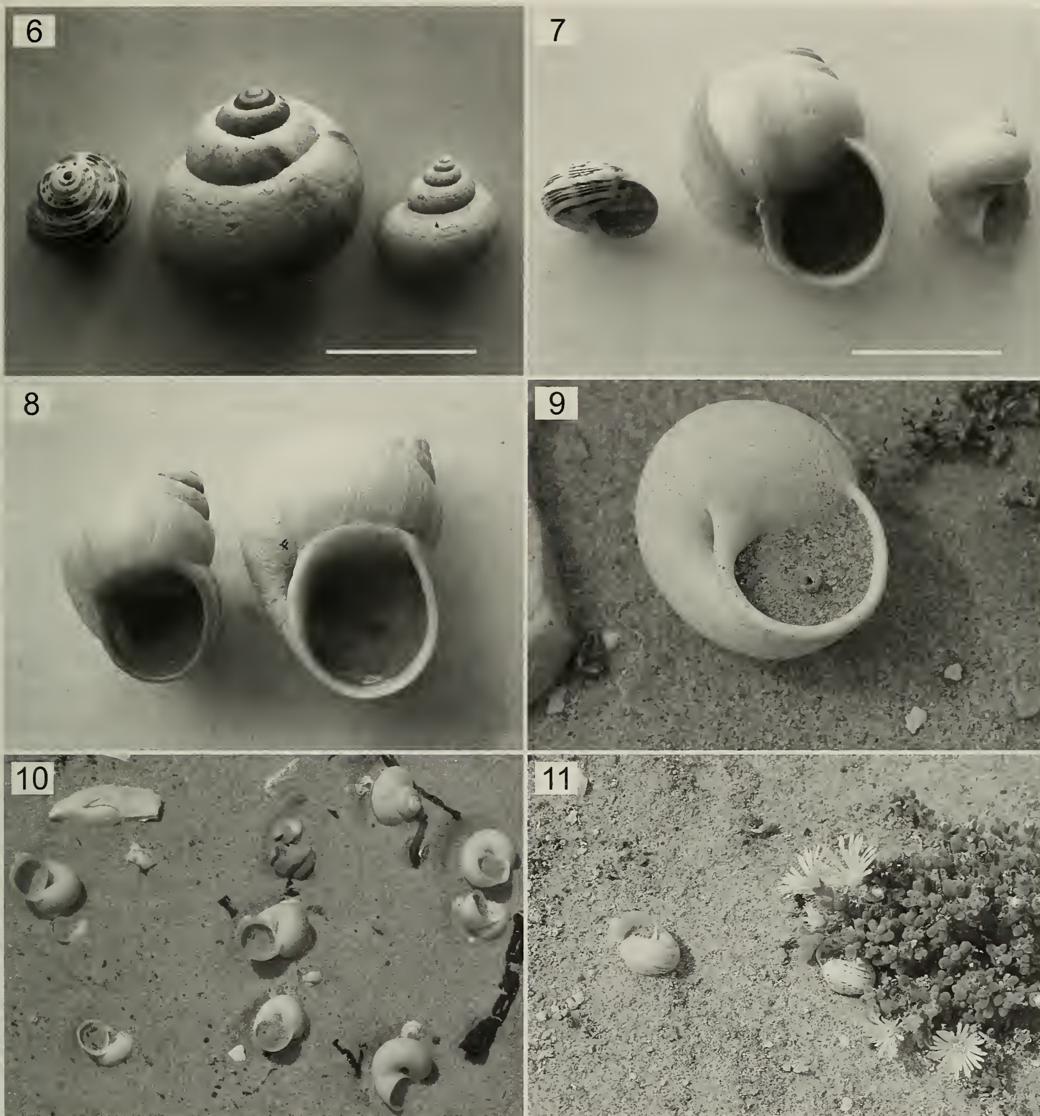
Fig. 5. Witsand, western south coast, sparsely vegetated dunes.

Trigonephrus (Dorcasiidae), *Tropidophora ligata* (Pomatidae), and an invasive exotic species, *Theba pisana* (Helicidae).

Trigonephrus shells are by far the largest with an altitude of 27–44 mm and a major diameter of 24–40 mm (Gess and Gess 1999). *Tropidophora ligata* shells are markedly smaller and therefore offer a cavity of considerably smaller volume but are similarly of greater altitude, 19.7 mm, than major diameter, 16.8 mm (Connolly 1938). *Theba pisana* are also of considerably smaller volume than *Trigonephrus* and in addition differ from both *Trigonephrus* and *Tropidophera* in having a low spiral, the altitude, 12.2 mm, being less than the major diameter, 17.0 mm (Connolly 1938).

In the winter rainfall area in southwestern Namibia and immediately south of the Orange River all snail shells encountered were of *Trigonephrus* and so samples from sites in this area are limited to shells of snails of this genus. At sites in the vicinity of Port Nolloth shells of *Theba pisana* were of equal or even greater abundance and were also sampled. From Port Nolloth south to Cape Town and east to Riet River in the Eastern Cape *Theba pisana* was abundant. *Trigonephrus* was not encountered east of Cape Town although one species, *Trigonephrus ambiguosus* (Fér.), has been recorded as far east as Mossel Bay (Connolly 1938, p. 238). *Theba pisana* was generally abundant to the eastern limit of sampling, at Riet River Mouth in the eastern Cape. *Tropidophora ligata* although recorded from as far west as the Cape Peninsula (Connolly 1938, p. 543) was found no further west than Port Elizabeth in the Eastern Cape, from where it was sampled at sites eastwards to Riet River.

Theba pisana is principally coastal Mediterranean in origin but also occurs in Switzerland, Ireland and southwestern Wales and England. It was apparently introduced into Cape Town from Europe circa 1881 (Connolly 1938, p. 269) from where it has spread north along the west coast, east (at least as far as East London, Mary Bursey pers. com.) along the south



Figs 6–11. 6–7, Shells (Mollusca, Gasteropoda) of *Tropidophora ligata* (Pomatiidae), *Trigonephrus* (Dorcasiidae) and *Theba pisana* (Helicidae) × 1 (scale bar = 2 cm). 8, Shells of two species of *Trigonephrus* to show variation in shell size. 9, Sand-filled shell of *Trigonephrus* showing entrance turret of *Quartinia* (Vespidae: Masarinae). 10, Sand-filled shells of *Tropidophora ligata*. 11, Sand-filled shells of *Theba pisana*.

coast, and in the west has invaded vineyards (Ferreira and Venter 1996) and citrus orchards (Joubert and Du Toit 1998). It has been the subject of considerable study in Israel, southern and western Australia and California, in which areas it is a serious agricultural pest (e.g. Arad and Avivi 1998, Baker 1988, Deisler and Stange 2005). Apart from damaging crops its copious slime production is considered to make infested plants unpalatable to stock and pollinators.

Sample size.—A sample size of 100 shells was chosen, however, sample size taken at some sites was smaller or larger than this number. For example smaller samples of *Trigonephrus* shells resulted from scarcity of shells at sites on the west coast in the vicinity of Cape Town or from the shortness of collection time for some stops in the Sperrgebiet (Diamond Area no. 1), southwestern Namibia, in which the authors were required to be part of a multidisciplinary group with varied agendas. Larger samples resulted either from the combination of several 100 shell samples from a single site or, in the case of *Theba pisana* and *Tropidophora ligata*, at sites, where incidence of use was very low, particularly along the south coast and eastwards, the decision to take larger samples.

Sampling method.—The area of sampling sites was not measured but was approximately 50 m by 50 m. Shells were collected by walking too and fro across the square and progessing from one side to the other. The shell samples were collected into sealed plastic bags. Later live insects which had escaped into the bags were captured and the shells were broken open and the contents examined. Live immatures were reared. Voucher specimens were deposited in the Albany Museum, Grahamstown.

Condition of material.—As snail shells in arid areas become bleached but do not degrade it is not possible to establish how long they have been available. Consequently, apart from active nests – nests containing live occupants – it is not possible to establish in what year the nests were constructed. The condition of nest material and dead occupants, however, varies considerably, from some nests being in a very poor or fragmentary state, so that it is clear that in a sample the nests are from a spread of years.

RESULTS

The results of the study, including published records, are presented in tabular form in the Appendix. Temporary lodgers, those occupants which use the shells only for sleeping and sheltering, have not been included. The present survey, however, confirmed the previous finding (Gess and Gess 1999) that there is a very low incidence of the use of shells for this purpose in daylight hours even in cold, wet weather. In the calculation of percentage of shells used empty and sandfilled shells are combined and a shell used by more than one occupant is counted only once.

In the desertic area from the Drachenberg in the north to Alexander Bay/ Brandkaros in the south 29 sites were sampled. All shells in this area were of *Trigonephrus* species. The percentage of used snail shells ranged from 33% (disregarding one exceptionally low percentage, 8%, obtained from near Kaizer's Camp to a remarkably high 92% (average 50%).

In the coastal sandveld from Port Nolloth in the north to Wallekraal to the south 11 sites were sampled. At all sites samples of *Trigonephrus* shells were taken. The percentage of shells used ranged from 40% to 100% (average 69%). In the Port Nolloth and Hondeklip Bay areas shells of *T. pisana* were present and at some sites were very much more abundant than those of *Trigonephrus.* In a sampling site five kilometres east of Port Nolloth a sample of 125 shells of *T. pisana* was taken with ease but only five shells of *Trigonephrus* were found in the same area. Only 25% of the shells of *T. pisana* had been used but all five *Trigonephrus* shells had been used. Similarly in a sampling site at Hondeklip Bay a sample of 121 *Theba pisana* shells was taken with ease but only 11 shells of *Trigonephrus* were found in the same area. Only 17% of the *T. pisana* shells had been used in contrast to 63% of the *Trigonephrus* shells.

At sites in the sandveld and coastal dune slacks to the south of Vanrhynsdorp south to Cape Town *Trigonephrus* shells were relatively uncommon, increasingly so southwards. The percentage of these shells used was consistently over 50% (56%–71%). Only two of the sites visited were free from *T. pisana*. One was an inland sandveld site southeast of Lutzville and the other was in the coastal dunes at Donkinsbaai. At these sites *Trigonephrus* shells were less common than at most of the northern sites but more common than at sites infested by *T. pisana.* At Lamberts Bay and a site north of Blaauwberg only nine and seven *Trigonephrus* shells were found but *T. pisana* was very common. Samples of 106, 130 and 134 shells of the latter were investigated. Of these only 18%, 24% and 12% had been used. At Elands Bay and Yzerfontein no *Trigonephrus* shells were found. *Theba pisana* shells were extremely abundant. Of the 147 shells from Elands Bay investigated only 21% had been used and of 200 and 256 shells from Yzerfontein investigated only 9% and 17% had been used.

Along the south and east coasts *Tropidophora ligata* has been recorded from the Cape Peninsula to Maputo (formerly Lorenzo Marques) (Connolly 1938), however, in the present study shells of this snail were found no further west than Port Elizabeth but the invasive exotic *T. pisana* was found to be extremely common in coastal sand dunes along the south coast east to Riet River Mouth, the most eastern site sampled. Use of snail shells along this section of the coast was very patchy. By far the greatest percentage use of *T. pisana* was at Witsand where there had been least disturbance by man but where building development was in full swing. At this site 48% of shells had been used. In the east the percentage of these shells used was 5.34% down to 0%.

Although *T. ligata* shells were abundant at some sites in the east the only site with an appreciable percentage, 19.9%, of used shells was at Kenton-on-Sea in a small area of dune slacks set aside as a bird sanctuary but now neglected and on the edge of housing development. At Salt Vlei, Port Alfred from which the use of these shells by a bee, *Wainia (Caposmia) elizabethae* was first recorded (as *Hoplitis* sp. in Gess and Gess 1988), ongoing building development initiated during the past decade has resulted in the destruction of the dune profile, the natural vegetation and associated snails and insects.

Much habitat destruction in many sandveld and coastal sites from Cape Town north along the west coast at least to Alexander Bay and along the south coast east to East London resulted from the introduction of the Australian *Acacia cyclops* A. Cunn. ex Loudon (Fabaceae: Mimosoideae) in the second half of the nineteenth century for the stabilization of sand flats and coastal dunes (Dennill et al. 1999). In seriously infested areas this shrub has formed extensive monospecific stands entirely replacing the species diverse natural vegetation.

Sand-filled shells.—Sand-filled shells in windswept areas offer within the spiral protected sites for the excavation of burrows. This habitat is widely utilized for this purpose by *Quartinia* (Vespidae: Masarinae) in the desertic areas of southwestern Namibia and the western Northern Cape southwards in the sandveld and supra-littoral dunes to Cape Town and eastwards at least to Witsand (Fig. 5). The only other occupant in this category encountered was *Tachysphex hermia* (Crabronidae: Larrinae), however, as only a single instance was recorded, in the Sperrgebiet, it seems that for this wasp this was unusual behaviour. Occasionally a shell used as a pre-existing cavity for nesting by a bee had later filled with sand and been used in addition as a sand-filled shell for nesting by a *Quartinia* (Fig. 17).

In their initial study Gess and Gess (1999) recorded the use of sand-filled snail shells for nesting by two undescribed species of *Quartinia.* Since then Gess (2007) has described seven species collected from nests in snail shells. Representation of species from snail shells was:

- in the desertic winter rainfall area north of the Orange River to south of Lüderitz Bay, *Q. obibensis* and *Q. refugicola* either singly or together;
- in the desertic winter rainfall area south of the Orange River to Hondeklip Bay, *Q. obibensis, Q. refugicola* and *Q. conchicola;*

- in sandveld in the vicinity of Hondeklip Bay and Wallekraal, *Q. namaqua* and *Q. namaquensis* (otherwise known only from the Kamiesberg);
- in the sandveld area north of Vanrhynsdorp, *Q. conchicola;*
- in dune slacks along the coast from Donkinsbaai, north of Lamberts Bay, south to 4 km north of Bloubergstrand in the Blaauwberg Conservation Area north of Cape Town, *Q. bonaespei;*
- at Yzerfontein on the southwest coast in addition, surprisingly, *Q. obibensis* and *Q. namaqua;*
- in dune slacks at Witsand on the south Coast east of Cape Town, *Q. australis.*

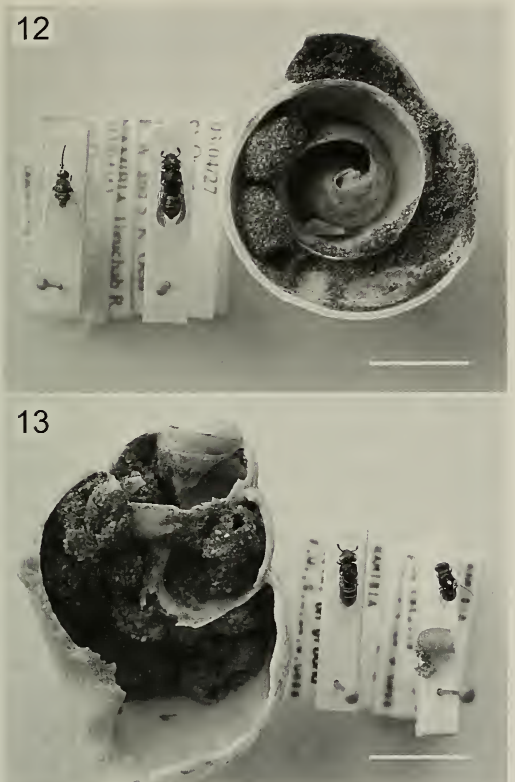
In the area north of Port Nolloth to south of Lüderitz , in addition to *Q. obibensis* and *Q. refugicola,* a third closely related species *Q. vexillata* Gess was collected from flowers at several sites but was not collected from snail shells. It has been suggested (Gess 2007) that this species most probably also nests in sand-filled snail shells.

All *Quartinia* nesting in snail shells stabilize their nest turrets, burrows and cell walls by the spinning together of sand grains with self-generated silk as first described for *Quartinia vagepunctata* Schulthess (Gess and Gess 1992). Where turrets were present they were of the short vertical or slightly curved form with diameter equal to that of the burrow as described and illustrated in Gess and Gess (1999) (Fig. 9). No species constructing bag shaped turrets such as are constructed by *Q. vagepunctata* (described and illustrated in Gess and Gess 1992) were found. Generally the shaft penetrates deep into the upper part of the spiral of the shell into which the cells are closely packed (Fig. 13), however, in some instances cell construction had been commenced lower in the spiral. The number of cells that can be constructed is limited by the volume of the shell. The number of cells per nest in the large, relatively high *Trigonephrus* shells can therefore be many times the number of cells per nest in small, relatively low *T. pisana* shells.

All species nesting in snail shells, except *Q. australis* for which no flower visiting records were obtained, visit flowers of "mesems" (Aizoaceae: Mesembryanthema). *Quartinia refugicola,* however, was collected more commonly from flowers of Asteraceae (eight genera) and also from flowers of Zygophyllaceae (*Zygophyllum*), Neuradaceae (*Grielum*) and Geraniaceae (*Sarcocaulon*), all characteristic of the desert areas where it occurs. *Quartinia bonaespei* in addition to "mesems" was collected from flowers of *Trachyandra* (Asphodelaceae) which is a characteristic plant of the supralittoral dunes of the Western Cape. Full flower visiting records are given in Gess (2007). Mating takes place on flowers.

As recorded in Gess and Gess (1999) *Tricholabiodes* sp. (Mutillidae: Sphaeropthalminae: Dasylabriini), an undescribed melanistic species of *Allocoelia* (Chrysididae: Chrysidinae: Allocoeliini) (Fig. 13) and a species of *Apolysis* (Bombyliidae: Usiinae: Usiini) (also in Greathead 1999) (Fig. 12) were reared from nests of *Quartinia* in snail shells from sites in the desertic areas immediately north and south of the Orange River.

Since 1999 further investigation of the "*Tricholabiodes*" specimens has revealed that only one of the specimens, a female, from southwest of Brandkaros was in fact *Tricholabiodes.* Three further females and a female each from southeast of Oranjemund and east of Alexander Bay are not of the genus *Tricholabiodes* but of an undescribed genus (Brothers pers. com. April 2007). Only one additional record of a mutillid, probably of one of these genera, from *Quartinia* cells has been obtained. The new record is for the Drachenberg, the most northern site at which *Trigonephrus* was encountered. It appears that the frequency of occurrence of mutillids in *Quartinia* nests in snail shells is low, only seven records having been obtained from 1,269 nests.



Figs 12–13. 12, Cells and female of *Quartinia obibensis*, and associated *Apolysis hesseana*, adult × 1.5 (scale bar = 2 cm). 13, Cells and female of *Quartina refugicola*, and associated *Allocoelia* n. sp., cocoon and imagine × 1.5 (scale bar = 2 cm).

Similarly the only new record of *Allocoelia* from *Quartinia* cells since the rearings from south of Rosh Pinah and east of Port Nolloth is from the Drachenberg. It is probable that it is present throughout the desertic areas to the south and north of the Orange River, however, it would appear that frequency of occurrence of *Allocoelia* in *Quartinia* nests in snail shells is low, only eight records having been obtained from 1,269 nests. *Allocoelia* pupates outside the *Quartinia* cell in which it developed so that in nests from which it has emerged its past presence is readily visible in the form of its empty cocoon attached to the outside of a *Quartinia* cell.

In 1999 the species identity of the *Apolysis* could not be established as only a pharate adult was available. It was considered that it was probably *A. capicola* Hesse (Greathead 1999). However, subsequent sampling of snail shells has provided adult female and male specimens from *Quartinia* nests from four additional sites from the Orange River north to the Klinghardtberge. The specimens have made it possible to determine the species as *Apolysis hesseana* (Greathead 2006). *Apolysis hesseana* was described briefly from a single denuded female specimen from the Northern Cape (Evenhuis and Greathead 1999) but the new material enabled a full description of the species to be given (Greathead 2006). In nests from which *Apolysis* has emerged the empty pupal cuticle is found attached to the outside of a *Quartinia* cell. It appears that frequency of occurrence of *Apolysis* in *Quartinia* nests in shells is low, only 14 records having been obtained from 1,269 nests but more frequent than by mutillids and *Allocoelia*.

Indeed overall in the areas sampled the frequency of parasitism of *Quartinia* nests in snail shells appears to be low, only 29 records having been obtained from 1,269 nests. It is of interest that no incidents of parasitism were recorded from south of Port Nolloth.

Empty shells.—empty snail shells were found to be utilized as nesting cavities by bees throughout the study area. The only other aculeate using the empty shells was *Alastor ricae* (Vespidae: Eumeninae) previously recorded (as "a eumenine", Gess and Gess 1999) from sites in the vicinity of Brandkaros to the south of the Orange River and presumed to be the same "Eumenid-wasp" referred to by Hesse (1944) as nesting in empty snail shells in "the very arid and sandy belt of the Namib desert". In subsequent sampling of snail shells by the present authors its nests have been found at 14 sites from north of the Orange River to the Drachenberg and a sample of snail shells collected by the BIOTA-Southern Africa Project at Grootderm to the south of the Brandkaros sites yielded two specimens (Koch 2006). Even without the presence of the nest builders the nests are readily identified being the only nests in shells with the nest closure constructed from pebbles embedded in a matrix of sand and an unidentified bonding substance (Fig. 14). In samples from which nests of *A. ricae* were obtained the percentage of shells used by this wasp was never more than 4%.

At the majority of sites along the west coast and in the desertic areas in the north the use of *Trigonephrus* shells by bees as nesting cavities was recorded. The percentage of shells used by bees at any one site ranged from 3% to 60%. All nests were of Megachilinae (Megachilidae) of the genera *Wainia (Caposmia), Hoplitis (Anthocopa)* (both Osmiini), *Afranthidium (Afranthidium)* (Anthidiini) or an unidentified anthidiine. Very little evidence was found of the use on the west coast of *T. pisana* shells for nesting by any of the bees, for all of which the cavity would be of too small a volume for successful nesting.

Two undescribed species of *Wainia (Caposmia)* were reared from nests in snail shells. Both are black with brown setae giving them an overall brownish hue and the gaster an indistinct brown banding, however, they are markedly different in size – Gess sp. C being 7 mm long (average of 5) and Gess sp. A 13 mm long (average of 10). The former was found only in desertic areas north of the Orange River and the latter from south of the Orange River southwards at least to Lamberts Bay. Both of these bees construct petal cells and seal the completed nest with a 5–7.5 mm thick hard, robust wall visible within the mouth of the shell (Gess and Gess 1999) (Figs. 15 and 16). This seal is multi-layered with each layer being constructed from a sheet of petal pieces over which is laid a firm sandy deposit, of which the bonding agent was not established.

One species of *Hoplitis (Anthocopa)* (Fig. 17) was reared from nests in snail shells. The cell walls are constructed from petals. Only the petals from a newly constructed nest in a *Trigonephrus* shell from the site south of Rosh Pinah were identified. They were cut from the pink petals of *Sarcocaulon* (Geranicaeae) (Gess and Gess 1999).

One species of *Afranthidium (Afranthidium), A. (A.) hamaticauda* Pasteels (Fig. 18), was found sheltering and nesting in *Trigonephrus* shells from the north of the study area south to Wallekraal. Previously (Gess and Gess 1999) the species of *Afranthidium* from snail shells north and south of the Orange River was tentatively identified as *A. (Oranthidium),* probably *odonturum* Cockerell and that sheltering in *Trigonephrus* shells at Wallekraal as *A. (A.) hamaticauda*. In a subsequent publication the former were erroneously named *Afranthidium (Afranthidium) ablusum* (Cockerell) (Gess and Gess 2007). The nests are readily distinguished from those of Osmiini as they are constructed from white, cottonwool-like, plant fibers (Gess and Gess 1999 and 2007) (Fig. 18). Similar anthidiine nests, but no bees, were in addition found in *Trigonephrus* shells from Lutzville further south.

The second species of anthidiine was found nesting in *Trigonephrus* shells at three sites, at Scorpion Mine, to the northwest of Scorpion Mine and in the Klinghardtberge. The bee is markedly larger than *A. (A.) hamaticauda*, the papillate cocoon being 13.3 mm by 8.1mm (average of four) compared with 7.7 mm by 4.3 mm (average of three), and the nests are constructed from golden-brown, not white, fibers (Fig. 19).

Along the south coast and to the east percentages of shells used by bees were low overall. Only one species of bee, *Wainia (Caposmia) elizabethae,* 9 mm long (average of 5), considerably smaller than the two western species, black with white setae, giving the gaster a distinct white banding, was recorded from Still Bay in the west to Riet River in the east. Both *T. ligata* and *T. pisana* shells are used, however, those of *T. ligata* for which the highest percentage use (12.3% at the Kenton-on-Sea bird sanctuary) was recorded seem to be preferred to those of *T. pisana*. It would appear that the low spiral of *T. pisana* is less suitable for nest construction than is the high spiral of *T. ligata*.

There was little evidence of parasitism in bee nests in snail shells. Chrysidid remains were extracted from two osmiine bee nests, one from Drachenberg and one from Aurus. The specimen from Drachenberg was a species of *Chrysis* of the *aestiva* group, possibly *C. grootdermensis*. *Chrysis grootdermensis* was described from one male which, together with eight *Hoplitis* (Megachildae: Osmiini) and two *Alastor* (Vespidae: Eumeninae), emerged from thirteen *Trigonephrus* shells, which had been collected at Groot Derm in the Richtersveld by members of BIOTA-Southern Africa and deposited in the Museum of Natural History, Berlin, Germany (Koch 2006). Koch suggested that, as the only species of the *aestiva* group, *C. interjecta* Du Buysson, for which biological data are available, emerged from a nest of *Anthidium lituratum* (Megachilidae), the specimen of *C. grootdermensis* might have been from the *Hoplitis* nest.

Numerous Eupelminae (Chalcidoidea: Eupelmidae) emerged from cocoons of *Wainia (Caposmia)* sp. C from a *Trigonephrus* shell from a site northeast of Kaiser's Camp and of *Wainia (Caposmia)* sp. A from a site southwest of Brandkaros.

Shells occupied by spiders.—The only residents, those occupants which not only use the shells as secure sites in which to build nests for rearing young but also "fit them out" as adult residences, were spiders of the families Clubionidae and Salticidae. The former were present at most sites and the latter, ant mimics, most notably at Wallekraal inland of Hondeklip Bay and at sites inland of Port Nolloth.

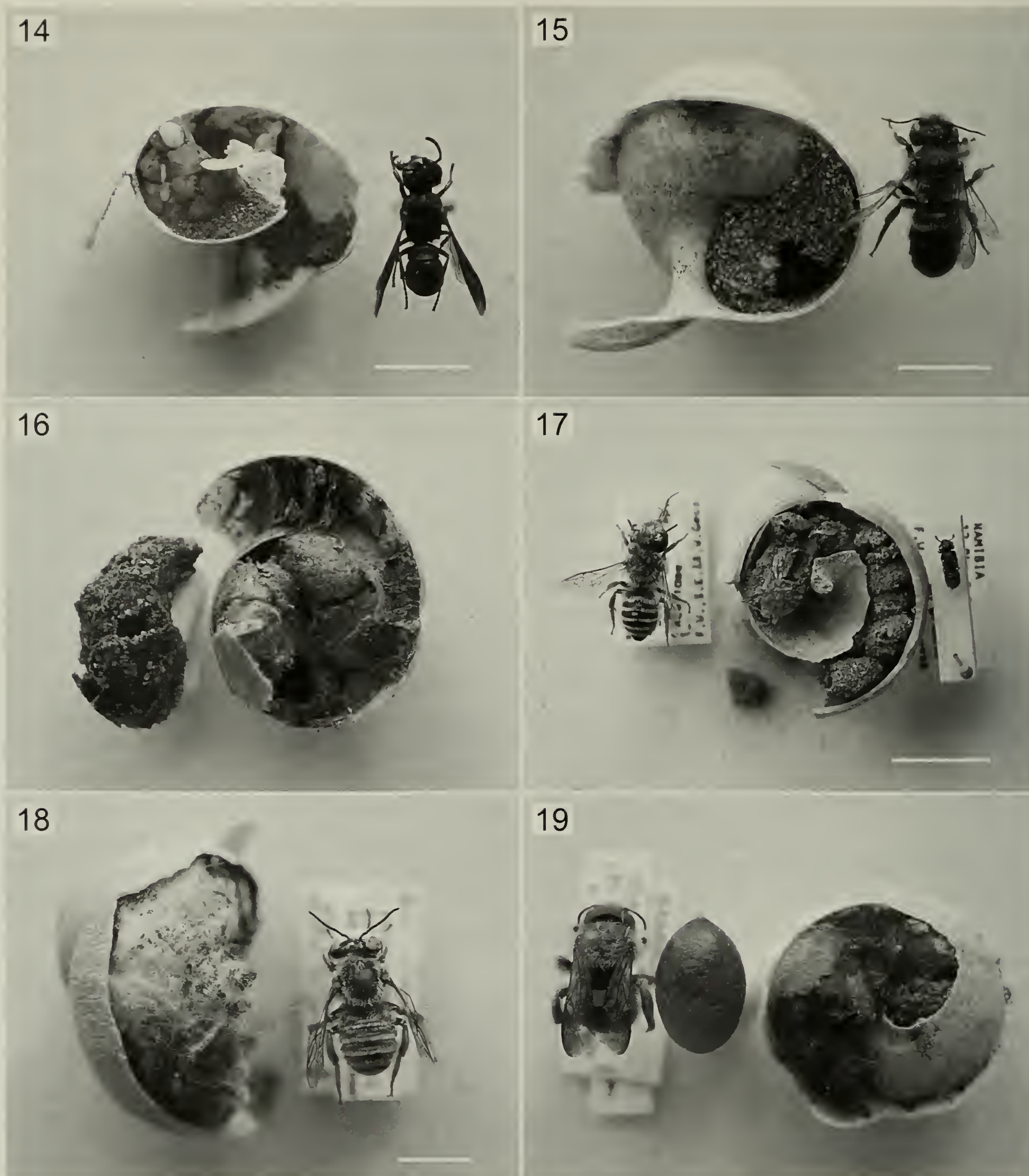
DISCUSSION

The shells of medium to large terrestrial snails, which are abundantly available, empty and sand-filled, in the desertic winter rainfall areas and the areas of sandy coastal dunes of southwestern Africa, offer abundant secure microhabitats in these areas of sparse low vegetation and unstable, often windswept sand. The investigations of such shells by Gess and Gess (1999 and thereafter) were sparked by the exciting discovery of nesting in sand-filled shells by ground nesting, silk-spinning *Quartinia* (Vespidae: Masarinae), representing a unique strategy for survival by a ground nester in such a habitat.

Although in windswept sandy areas, where the ground is unstable, sand-filled snail shells represent the only microhabitat offering a secure nesting site for *Quartinia*, where rock outcrops occur, pockets of sand offer additional secure nesting sites. That such sites may be used by snail shell nesters was confirmed by the discovery of *Q. refugicola* nesting in sand trapped in calcrete in addition to sand trapped in *Trigonephrus* shells (Gess and Gess 1999). It is therefore clear that for *Q. refugicola*, at least, nesting in snail shells is not obligatory. It seems probable that this will be found to be the case for at least some of the other species collected from nests in snail shells.

The use of empty snail shells as pre-existing nesting cavities by osmiines is known from the Nearctic, Palaearctic, Britain, Central Europe, the Mediterranean, Eurasia and Japan and by an anthidiine from the Mediterranean into Asia Minor (O'Toole and Raw 1991, Bellman 1995) in a variety of habitats. The use of empty snail shells by aculeates (osmiines, anthidiines and a eumenine) in the desertic and coastal areas of southern Africa does not therefore represent a desert survival strategy. It is, however, of note that nesters of this category were found to be more diverse and more abundant in the winter rainfall desertic areas than they were in the coastal areas.

Not surprising is the wide use of shells as lodgings and nesting sites by spiders.



Figs 14–19. 14, *Alastor ricae* (Vespidae:Eumeninae) with pebble and matrix cell closure in cut open *Trigonephrus* shell × 1.5 (scale bar = 2cm). 15, *Wainia (Caposmia)* species A (Megachilinae: Osmiini) and nest entrance closure with exit hole × 1.6 (scale bar = 2 cm). 16, Nest of *Wainia (Caposmia)* species A with nest closure removed to one side.17, *Hoplitis (Anthocopa)* sp. (Megachilinae: Osmiini) and *Quartinia refugicola* with cut open shell of *Trigonephrus* to show a cell of the former in the peek of the spiral followed by cells of the latter × 1.5 (scale bar = 2 cm). 18, *Afranthidium (Afranthidium) hamaticauda* (Megachilinae: Anthidiini) with white plant fiber nest in cut open *Trigonephrus* shell × 2 (scale bar = 2 cm). 19, Anthidiine species 2 with cocoon and nest in cut open *Trigonephrus* shell × 1.5.

Spiders are not always the initial occupiers of shells but in many instances were found to have moved into shells already occupied by wasps or bees, which were either actively nesting or had completed nesting. Clearly, when nesting was still in progress, the occupation by a spider will have terminated nesting and, when nests had been completed but emergence of offspring had not yet taken place, presence of a spider will have been hazardous for exiting by imagines. Considering that in the desert where a sea mist rolls in from the west coast in the evenings and persists well into the morning and where the mid-day heat is often extreme it is surprising that the use of the shells for sheltering during these times seems to be minimal. Also surprising is the low level, in most areas, of parasitism of the wasps and bees by insects feeding on the immatures or the provision.

Clearly, the marked difference in volume of the large shells of *Trigonephrus* with a western distribution and the much smaller shells of *Tropidophora ligata* with a southern to eastern distribution must make a difference to the suitability of the cavity offered. This may explain the greater percentages of shells used and the larger number of bee species and *Quartinia* species using shells where *Trigonephrus* shells are available as compared to the south and southeast where they are not available. This possibility is supported by the fact that where the invasive snail *Theba pisana*, having shells with a relatively small volume and low spiral, has all but replaced *Trigonephrus* percentage use of *T. pisana* is very low compared with *Trigonephrus*. Indeed in areas of increasing abundance of *T. pisana* at the expense of *Trigonephrus* a drop in populations of snail shell users may be expected, which would in all probability adversely affect pollination of at least some of the plants visited and thus have a cascade effect. In addition in some areas ongoing spread of *Acacia cyclops* and coastal development pose a threat both to snails and snail shell nesters as it forms monospecific stands which replace the diverse natural vegetation on which they depend.

The division of snail shells into empty and sand-filled does not suggest that either state has any permanence. In windswept sandy areas the duration of either state is dictated by the intervals between gale force winds. During these quiet periods cavity nesting wasps or bees will seek out empty shells in which to nest and excavators in friable soil will seek out suitable sites for nesting. It is clear from the survey that the only regular nesters in this latter category are *Quartinia* species and that their nests are commonly found in snail shells throughout the winter rainfall desertic areas, at some sites in the sandveld and at many in the coastal dune slacks on the west coast and along the south coast eastwards at least as far as Still Bay. The probable explanation is their ability to spin silk. In nest building the silk is initially used to stabilize sand grains in the excavation of a burrow and the construction of a nest turret. The silk lined burrow reaches far into the shell where cell construction from sand and silk takes place safely in the spiral of the shell where the cells can be securely packed and attached to the shell. As is clear from shells collected into plastic bags, the sand matrix is often not stable and easily falls out of the shells together with the entrance turret and burrow. Thus when the next gale blows, tumbling the shells, some at least of the sand-filled shells containing *Quartinia* cells will empty of all but the cells and some at least of the empty shells containing the nests of cavity nesting wasps and bees will fill with sand. It is therefore not surprising that in some shells a few bee cells were found in the peak of the spiral followed by *Quartinia* cells and in others a few *Quartinia* cells were found in the peak followed by bee cells. Furthermore, *Quartinia* cells found in otherwise empty shells do not suggest that the builder, like the cavity nesters, brought building materials into an empty shell. In the earlier investigation two species of *Quartinia* were found to be involved. In the present survey seven species have been found nesting in this way. However, it is of note that in some areas where one or more of these *Quartinia* species has been found nesting in snail shells additional species, not found nesting in shells, have been collected visiting flowers. These were all species with incomplete venation, formerly of the genus *Quartinioides* Richards now included in *Quartinia* (following van der Vecht and Carpenter 1990). In all instances this was where rocky outcrops were present or the vegetation was less sparse.

ACKNOWLEDGEMENTS

Grateful thanks are expressed to: all those who gave access to their land or land in their care; all those bodies who issued permits for the collection of insects and plant samples, namely Cape Nature, Western Cape Nature Conservation Board – City of Cape Town for the Blaauwberg Conservation Area – Department of Nature and Environmental Conservation, Northern Cape – Department of Economic Affairs, Environment and Tourism, Eastern Cape, Western Region – Ministry of Environment and Tourism, Namibia – Ministry of Mines and Energy, Namibia for the Sperrgebiet (Diamond Area no. 1); Ms Coleen Mannheimer of the National Herbarium of Namibia, Windhoek for her invitations to join the Herbarium party on their expeditions to the Sperrgebiet in 2002, 2003 and 2005 and also for her determination of voucher specimens of Namibian plants; Mr Robert W Gess for field and laboratory assistance in 1996; Mr David W Gess, Ms Gaby Gess and Miss Gaby Maria Gess for field assistance at Melkbosstrand in 2005 and Yzerfontein in 2006; Dr David J Greathead, Centre for Population Biology, Imperial College London, for the identification of *Apolysis hesseana* Evenhuis and Greathead (Diptera: Bombyliidae); Professor Denis Brothers, Department of Entomology, University of KwaZulu-Natal, for his comments on the mutillids (Hymenoptera: Mutillidae); Ms Mary Bursey, East London Museum for the record of *Theba pisana* (Müller) (Helicidae) from East London; Dr Dai Herbert, Natal Museum for providing references to *Theba pisana* as an agricultural pest in South Africa; Ms Bronwyn McLean and Ms Debi Brody of the Graphic Services Unit, Rhodes University for assistance with the preparation of the figures for publication; the editor and the two reviewers for their constructive comments; the National Research Foundation of South Africa (NRF) for running expenses grants; and the Board of Trustees of the Albany Museum for Research Contracts granted to the authors since 2003, which have given the authors continued use of the museum's facilities since their retirements.

LITERATURE CITED

Arad, Z. and T. R. Avivi. 1998. Ontogony of resistence to dessication in the bush-dwelling snail *Theba pisana* (Helicidae). *Journal of Zoology London* 244: 515–526.

Baker, G. H. 1988. Dispersal of *Theba pisana* (Mollusca: Helicidae). *Journal of Applied Ecology* 25: 889–900.

Bellman, H. 1995. *Bienen, Wespen, Ameisen.* Franckh-Kosmos, Stuttgart. 336 pp.

Connolly, M. 1938. A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum* 33: 1–660.

Deisler, J. E. and L. A. Stange. 2005. White Garden Snail, *Theba pisana* (Mueller) (Gasteropoda: Helicidae) at http://edis.ifas.ufl.edu.

Dennill, G. B., S. K. Donnelly, and F. A. C. Impson. 1999. Insect agents used for the biological control of Australian *Acacia* species and *Paraserianthes lophanta* (Willd.) Nielsen (Fabaceae) in South Africa. *African Entomology* Memoir No. 1: 45–54.

Evenhuis, N. L. and D. J. Greathead. 1999. *World Catalogue of bee flies (Diptera: Bombyliidae).* Backhuys, Leiden. xlviii + 756 pp.

Ferreira, J. H. S. and E. Venter. 1996. *Grapevine diseases, pests and abnormalities in South Africa.* ARC-Nietvoorbij Institute for Viticulture and Oenology, Stellenbosch.

Gess, F. W. 2007. The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part I. Descriptions of new species with complete venation. *Journal of Hymenoptera Research* 16: 211–233.

——— and S. K. Gess. 1988. Terrestrial invertebrates: Insects. Pp. 241–250 *in*: Lubke, R. A., F. W. Gess, and M. N. Bruton, eds. *A field guide to the Eastern Cape coast*. Grahamstown Centre of the Wildlife Society of Southern Africa, Grahamstown.

——— and S. K. Gess. 1992. Ethology of three southern African ground nesting Masarinae, two *Celonites* species and a silk spinning *Quartinia* species, with a discussion of nesting by the subfamily as a whole (Hymenoptera: Vespidae). *Journal of Hymenoptera Research* 1: 145–155.

——— and S. K. Gess. 1998. Terrestrial Invertebrates: Insects. Pp. 344–354 *in:* Lubke, R. A., and I. De Moor, eds. *A Field Guide to the Southern and Eastern Cape Coast*. Cape Town University Press and Grahamstown Centre of the Wildlife Society of Southern Africa, Cape Town.

——— and S. K. Gess. 1999. The use by wasps, bees and spiders of shells of *Trigonephrus* Pilsbry. (Mollusca: Gasteropoda: Dorcasiidae) in desertic winter-rainfall areas in southern Africa. *Journal of Arid Environments* 43: 143–153.

Gess, S. K. and F. W. Gess. 2007. Notes on the nesting and flower visiting of anthidiine bees (Hymenoptera: Megachilidae: Megachilinae: Anthidiini) in southern Africa. *Journal of Hymenoptera Research* 16: 30–50.

Greathead, D. J. 1999. *Apolysis* sp. (Diptera: Bombyliidae) reared from *Quartinia* sp. (Hymenoptera: Vespidae: Masarinae). *Journal of Arid Environments* 43: 155–157.

———. 2006, New records of Namibian Bombyliidae (Diptera) with notes on some genera and descriptions of new species. *Zootaxa* 1149: 3–27.

Hesse, A. J. 1944. *A guide book to the exhibits of insects.* South African Museum, Cape Town. 47 pp.

Joubert, P. H. and W. J. Du Toit. 1998. Snails and slugs on citrus In: *Citrus pests in the Republic of South Africa.* Institute for Tropical and Subtropical Crops. ARC/LNR, South Africa.

Koch, F. 2006. Snail shells (Mollusca, Gasteropoda, Dorcasiidae) as microhabitats in South African deserts, with the description of a new chrysidid wasp (Insecta, Hymenoptera, Chrysididae) discovered by BIOTA-Southern Africa Project. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe* 82: 191–197.

O'Toole, C. and A. Raw. 1991. *Bees of the world.* Blandford, London. 192 pp.

Vecht, J. vander and J. M. Carpenter. 1990. A catalogue of the genera of the Vespidae (Hymenoptera). *Zoologische Verhandelingen* 260: 1–62.

APPENDIX

Available data on the use of snail shells in the semi-arid to arid areas of southern Africa. Collectors' numbers are those of F.W.Gess and S.K.Gess. Other collectors are given by name.

Taxa in order of table headings: -

Shell ID (Mollusca, Gasteropoda): Dorcasiidae – *Trigonephrus* Pilsb. (Figs. 6–9); Pomatiidae – *Tropidophora ligata* (Müll) (Figs. 6, 7 and 10); Helicidae – *Theba pisana* (Müll) (Figs. 6, 7 and 11).

Masarinae (Vespidae): *Quartinia* Ed. André, *australis* Gess, *bonaespei* Gess, *conchicola* Gess, *namaqua* Gess, *namaquensis* Gess, *obibensis* Gess (Fig. 12), *refugicola* Gess (Fig. 13).

Chrysididae: A. = *Allocoelia* n. sp. (Fig. 13), C. g. = *Chrysis grootdermensis* Koch; C. ? g. = *Chrysis* (*aestiva* group) ? *grootdermensis;*

Bombyliidae: *Apolysis hesseana* Evenhuis and Greathead (Fig. 12).

Eumeninae (Vespidae): *Alastor ricae* Giordani Soika (Fig. 14).

Mutillidae: T. = *Tricholabiodes* n. sp.; n. genus.

Megachilidae, Megachilinae: Osmiini – W. (C.) = *Wainia (Caposmia)* Peters, W. (C.) e. = *W. (C.) elizabethae* Brauns, *W. (C.)* sp. A, *W. (C.)* sp. C. (Figs. 15 and 16) and H. (A.) = *Hoplitis (Anthocopa)* Lepeletier and Serville (Fig. 17); Anthidiini – A.(A.) h. = *Afranthidium (Afranthidium) hamaticauda* Pasteels (Fig. 18) and anthidiine sp. 2 (Fig. 19).

Spiders: Clubionidae and Salticidae

Additional taxa: -

*Crabronidae: Larrinae: *Tachysphex hermia* Arnold; ** Eupelminae (Chalcidoidea: Eupelmidae) from cocoons of *Wainia (Caposmia).*

Appendix.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
Drachenberg seaward side 27.05S 15.25E 05/06/21	Trigonephrus 90 70%	50 55.6%	C.?g. in megachilid nest 1		1♀ ex Quartinia cell	9 10%	4 4.4%	12 13.3%
Drachenberg landward side 27.05S 15.25E 05/06/15	Trigonephrus 44 60%	17 38.6%	A. in Quartinia nest 1			8 18.2%	2 4.5%	6 13.6%
Sperrgebiet main rd 27.14S 15.28E* 02/03/6a	Trigonephrus 29 65.5%	10 34%				A. (A.) h. ? W. (C.) ? H. (A.) 4 13.8%		7 24%
W Klinghardtberge NW Heioab 27.17S 15.36E 03/04/64	Trigonephrus 61 63.9%	obibensis 34 55.7%				2 3.3%	1 1.6%	17 27.9%
Klinghardt's Basin 27.19S 15.46E 05/06/24	Trigonephrus 60 66.7% used	obibensis + refugicola 30 50%		1		anthidiine 2 13 21.7%	1 1.6%	
Klinghardtberge 27.19S 15.46E 05/06/29	Trigonephrus 53 75.5%	obibensis 37 69.8%				W. (C.) sp. C 13 24.5%		
Klinghardtberge 27.19S 15.47E 05/06/34	Trigonephrus 36 91.7%	30 83.3%				? 10 27.8%		
Sperrgebiet main rd 27.23S 15.32E 02/03/7a	Trigonephrus 19 63.2%	6 31.6%				? W. (C.) ? H. (A.) 4 21.1%	2 10.5%	
Nomitsas 27.27S 15.52E 02/03/21	Trigonephrus 32 65.6%	refugicola 13 40.6%				? W. (C.) ? H. (A.) 11 34.4%		
SE Heioab 27.27S 16.06E 03/04/48	Trigonephrus 30 70%	19 63.3%				7 23.3%	1 3.3%	

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
Othona "forest"	Trigonephrus					(mud walls – 1 0.5%		
27.29S 16.10E								
03/04/47	223 36.8%	79 35.4%		1 0.5%		8 3.6%	1 0.5%	
nr Kaizer's Camp	Trigonephrus	obibensis						
27.30S 15.44E**								
05/06/22&23	88 8%	4 4.5%				3 3.4%		
Uguchab River bed	Trigonephrus	refugicola						
27.31S 16.12E								
03/04/43	227 54%	103 45.4%		7 3.1%		35 15.4%	4 1.8%	2 0.8%
Aurus	Trigonephrus		chrysidid in					
27.36S 16.22E			bee nest					
03/04/37	145 57.2%	53 36.6%	2			43 29.7%	1 0.7%	5 3.4%
E Aurus	Trigonephrus							
27.36S 16.23E								
03/04/38	113 62.8%	66 58.41%				9 7.96%		
E Aurus	Trigonephrus					(mud walls – 8 4.9%)		
27.37S 16.25E								
03/04/39	53 32.5%					37 22.7%	2 1.2%	
Chamnaub	Trigonephrus							
27.43S 16.05E								
02/03/8	20 85%	9 45%						12 60%
Chamnaub	Trigonephrus					? W. (C.)		
27.43S 16.05E						? H. (A.)		
02/03/12	20 70%	7 35%				6 30%		7 35%
NW Scorpion Mine	Trigonephrus	obibensis				anthidiine 2		
27.45S 16.32E								
03/04/35	102 58.8%	54 52.9%		3 2.9%		15 14.7%		8 7.8%
Scorpion Mine	Trigonephrus	obibensis				anthidiine 2		
27.49S 16.35E								
03/04/33	105 55.2%	29 27.6%				13 12.3%		
Red Dune, Obib	Trigonephrus							
27.55S 16.39E								
03/04/32	100	7 7%				12 12%	1 1%	1 1%
Obib hut site	Trigonephrus	obibensis						
28.00S 16.39E								
03/04/27	170 73.1%	100 58.8%				33 19.4%	3 1.8%	8 4.7%

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
SSW Boegoeberg 28.00S 15.52E 02/03/16	Trigonephrus 55 72.7%	 17 30.9%				A. (A.) h. ? W. (C.) ? H. (A.) 8 14.5%	1 1.8%	11 20%
S Rosh Pinah 28.03S 16.51E 96/97/59,61, 63-77	Trigonephrus 17 100%	refugicola + obibensis 17 100%	A. in Quartinia nest 3			?H. (A.) sp. 1 ?W. (C.) 1		
S Rosh Pinah 28.03S 16.51E 96/97/60, 62, 78-81, 84	Sand filled cavities in calcrete 6	refugicola 7	A. in Quartinia nest 3					
Red Dune, Obib 28.08S 16.42E 03/04/29	Trigonephrus 118 46.6%	refugicola 43 36.4%				 16 13.6%		
Red Dune, Obib 28.08S 16.42E 03/04/30	Trigonephrus 104 67.3%	 39 37.5%				W. (C.) sp. C 36 34.6%	3 2.9%	5 4.8%
E Oranjemund 28.26S 16.42E 97/98/67	Trigonephrus 13 84.6%	refugicola 11 84.6%		1 7.7%		? W. (C.) ? H. (A.) 2 15.4%		
SW Brandkaros 28.29S 16.40E 96/97/99-108A	Trigonephrus 36 75%	refugicola 14 38.9%				A. (A.) h. H. (A.) sp. 1 5 11.1%	1 2.8%	1 2.8%
SW Brandkaros 28.29S 16.40E** 96/97/131-152	Trigonephrus 47 89.4%	refugicola obibensis conchicola 31 66%				W. (C.) sp. A H. (A.) sp. 1 7 14.9%	1 2.1%	5 10.6%
SW Brandkaros 28.29S 16.40E 96/97/160-162	Trigonephrus 23 78.3%	 13 56.5%			T. ex Quartinia cell 1 ♀ new genus Ex Quartinia cells 3 ♀	W. (C.) sp. A 8 34.8%	2 8.7%	
E Oranjemund 28.30S 16.36E 97/98/36	Trigonephrus 73 43.8%	refugicola 23 31.5%				A. (A.) h. ? W. (C.) ? H. (A.) 5 6.8%		

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
SE Oranjemund	Trigonephrus	conchicola			new genus	A. (A.) h.		
28.35S 16.30E					Ex Quartina			
96/97/95-98	4	2			cells 1 ♀	1		
Groot Derm	Trigonephrus		C. g.			Hoplitis sp.		
NE Alexander Bay								
28.37S 16.40E								
BIOTA-SA	13		1 emerged			8 emerged	2 emerged	
E Alexander Bay	Trigonephrus				new genus	A. (A.) h.		
28.38S 16.28E					ex Quartina			
96/97/95-98	4	3			cells 1 ♀	1		
N Port Nolloth	Trigonephrus	refugicola				A. (A.) h.		
28.47S 16.38E		conchicola						
97/98/77B	14 78.6%	5 35.7%				3 21.4%		2 14.3%
N Port Nolloth	Trigonephrus							
28.50S 16.40E								
96/97/169	25 40%	7 28%						2 8%
5km E Port Nolloth	Theba pisana							
29.15S 16.53E								
05/06/81	125 24.8%	19 15.2%						12 9.6%
5km E Port Nolloth	Trigonephrus					?		
29.15S 16.53E								
05/06/82	5 100%	1 15%				2 40%		5 100%
Port Nolloth	Trigonephrus					?		
29.16S 16.53E								
05/06/83	26 53.8%	6 23%				6 23%		6 23%
Port Nolloth	Theba pisana							
29.16S 16.53E								
05/06/83	64 14.1%	3 4.6%						6 9.4%
Port Nolloth	Trigonephrus					W. (C.) sp. A		
29.16S 16.53-54E						A. (A.)		
05/06/89	10 80%	1 10%				4 40%		4 40%
E Port Nolloth	Trigonephrus							
29.16S 16.54E								
05/06/84	86 38.4%	23 26.7%						8 9.3%

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
E Port Nolloth	Trigonephrus		A.					
29.16S 16.55E			in Quartinia nest					
97/98/79	18 50%	4 22.2%	1 5.6%					2 11.1%
6km E Port Nolloth	Trigonephrus					?		
29.16S 16.55E								
05/06/78	28 82.1%	12 42.9%				7 25%		16 57.1%
E Hondeklip Bay	Trigonephrus	namaqua				? osmiine		
30.19S 17.17E								
05/06/87	11 63.6%	5 45.5%				3 27.3%		
E Hondeklip Bay	Theba pisana	namaqua				? osmiine		
30.19S 17.17E								
05/06/87	121 17.4%	9 7.4%				3 2.5%		10 8.3%
W Wallekraal	Trigonephrus	namaquensis				anthidiine		
30.21S 17.26E		conchicola						
97/98/146	58 84.5%	15				22		9
W Wallekraal	Trigonephrus					A. (A.) h.		
30.22S 17.27E						W. (C.) sp.A		
97/98/143	79 81%	12 15.2%				44 55.7%		8 10.1%
W Wallekraal	Trigonephrus	namaqua				W. (C.) sp. A		
30.22S 17.28E								
05/06/88	60 93.3%	12 20%				36 60%		26 43.3%
N Vanrhynsdorp	Trigonephrus					? W. (C.)		
31.30S 18.43E								
96/97/178	34 71.4%	4 11.8%				1 2.9%		7 20.6%
N Vanrhynsdorp	Trigonephrus	conchicola				? osmiine		
31.31S 18.43E								
05/06/90	127 39.4%	38 29.9%				4 3.1%		8 6.3%
N Vanrhynsdorp	Trigonephrus							
31.31S 18.43E	Small							
05/06/90	59 16.9%	c 6 10.2%						c 6 10.2%
SE Lutzville	Trigonephrus	conchicola				anthidiine		
31.36S 18.23E								
05/06/98	59 61%	10 16.9%				12 20%		14 23.7%

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
Donkinsbaai	Trigonephrus	bonaespei				W. (C.)		
31.54S 18.17E								
05/06/95	35 71%	22 65.7%				2 5.7%		1 2.9%
Lamberts Bay	Trigonephrus	bonaespei				W. (C.) sp. A		
32.05S 18.19E								
05/06/93	9 55.6%	3 33.3%				2 22.2%		
Lamberts Bay	Theba pisana							
32.05S 18.19E								
05/06/93	106 17.9%	5 4.7%						13 12.3%
Elands Bay	Theba pisana	bonaespei						
32.19S 18.20E								
05/06/109	147 21.1%	4 2.7%				1 0.7%		26 17.7%
Roscherpan Nat. Res.	Trigonephrus	bonaespei						
32.36S 18.18E								
Feurer & Thell		4 ♀♀, 1 ♂						
Yzerfontein	Theba pisana	bonaespei				?		
33.20S 18.10E		obibensis						
DW, GT & GM Gess		namaqua						
	200 9.5%	6 3%				1 0.5%		12 6%
Yzerfontein	Theba pisana					?		
33.20S 18.10E								
06/07/14	256 16.8%	12 4.6%				3 1.17%		28 10.94%
Melkbosstrand	Theba pisana	bonaespei						
33.42S 18.26E								
05/06/119	155 20.6%	7 4.5%						23 14.8%
Melkbosstrand	Helix aspersa							
33.42S 18.26E								
05/06/119	1	1						
N Bloubergstrand	Trigonephrus	bonaespei						
33.46S 18.27E								
05/06/110+112	7 57.1%	3 43%						1 14.3%
N Bloubergstrand	Theba pisana							
33.46S 18.27E								
05/06/110	130 23.8%	12 9.2%				9 6.9%		12 9.2%
N Bloubergstrand	Theba pisana	bonaespei						
33.46S 18.27E								
05/06/112	134 11.9%	3 2.2%						13 9.7%

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
N Bloubergstrand	Helix aspersa							
33.46S 18.27E								
05/06/112	3							
Bloubergstrand	Theba pisana							
33.46S 18.27E								
02/03/99	25 32%	2 8%						6 24%
Still Bay	Theba pisana					W. (C.) e.		
34.22S 21.27E								
02/03/104	388 6.7%					5 1.3%		20 5.2%
Witsand	Theba pisana	australis						
34.23S 20.52E								
02/03/101	69 48%	16 23.2%						17 24.6%
Wilderness	Theba pisana					? W. (C.)		
34.00S 22.39E								
02/03/103	85 26%					3 3.5%		15 21.7%
Maitland River Mouth	Tropidophora ligata							
33.59S 25.17E	254 3.94%							10 3.94%
06/07/16	Theba pisana 3 0%							
	Achatina 3 0%							
Sardinia Bay	Theba pisana					?		
34.02S 25.32E								
06/07/5	337 5.34%					1		17 5.04%
Sardinia Bay	Tropidophora							
34.02S 25.32E	ligata							
06/07/6	202 1.49%							3 1.49%
Bluewater Bay	Theba pisana							
33.51S 25.38E								
06/07/8	200 0%							
Bluewater Bay	Tropidophora							
33.51S 25.38E	ligata							
06/07/8	300 0%							
Boknes	Tropidophora							
33.45S 26.35E								
06/07/9	100 0%							
Boknes	Tropidophora							
33.45S 26.35E	ligata							
06/07/10	380 1.58%							6 1.58%

Appendix. Continued.

Site collectors' no.	Shell ID no & % used	Masarinae nesting in sand-filled shells	Chrysididae "parasites"	Bombyliidae "parasites"	Mutillidae "parasites"	Megachilidae nesting in empty snail shells	Eumeninae nesting in empty snail shells	Spiders residents
Kenton-on-Sea	Tropidophora ligata					Remains of bee nest		
33.42S 26.40E								
06/07/1	100 5%					2 2%		
Kenton-on-Sea	Tropidophora ligata					Remains of bee nests		
33.42S 26.40E						and bees		
06/07/2						W (C.) ?e.		
	106 17.9%					13 12.3%		5 4.7%
Port Alfred	Tropidophora ligata					W. (C.) e.		
E. Mc C. Callan								
1979 in Gess and Gess						5 emerged		
1988								
Port Alfred, Salt Vlei,	Tropidophora ligata,							
habitat destroyed by	4 0%							
housing development								
33.37S 26.53E	Helix aspersa							
06/07/4	2 0%							
Riet River Mouth	Tropidophora ligata					W (C.) ?e.		
33.34S 27.01E								
06/07/3	41 7.3%					2 4.9%		
Riet River Mouth	Theba pisana							
33.34S 27.01E								
Kaltenpoth	300 4%					3 1%		9 3%